The Mountain Pine Beetle and Whitebark Pine Waltz: Has the Music Changed?

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Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae) (MPB), is a bark beetle native to western North American forests, spanning wide latitudinal and elevational gradients. MPB infest and reproduce within the phloem of most *Pinus* species from northern Baja California in Mexico to central British Columbia in Canada, and their geographic range is dictated by the distribution of both suitable host species and favorable climatic regimes (Safranyik 1978, Logan and Bentz 1999).

Whitebark pine (*Pinus albicaulis* Engelmann), a long-lived species within the pine subsection *Cembrae*, is typically found just below the alpine timberline (McCaughey and Schmidt 2001). MPB has existed at detectable levels in high elevation whitebark pine stands for some time. Paleoecological records suggest that *Dendroctonus spp*. were present in ecosystems dominated by whitebark pine during the Holocene (Brunelle et al. *submitted*). Dendroecological and written records also indicate that MPB population outbreaks occurred in high elevation stands during the 1930 to 1940 time period (Perkins and Swetnam 1996, Furniss and Renkin 2003 and references therein). Periods of beetle-caused mortality during the 20th century were associated with warmer than average temperatures, and documented in historical records as ephemeral. Following periods of warm temperature, MPB populations returned to endemic levels with the return of cooler temperatures. In general, it was believed that cold temperatures in high elevation whitebark pine forests were not conducive to MPB outbreaks, often resulting in life-cycles requiring three years to complete (Amman 1973).

Many life-history strategies that drive MPB outbreak dynamics are strongly influenced by temperature. Successful MPB reproduction requires death of its host. Host trees, however, have evolved effective response mechanisms against bark beetle attacks (Raffa et al. 1993). Almost all trees respond to bark beetle attacks, but only those with a rapid and sustained response survive. Tree defensive mechanisms can be exhausted if many beetles attack the same tree simultaneously. Outcomes of MPB dispersal and colonization attempts, therefore, depend on competing rate reactions regulating both beetle arrival and host tree resin response (Raffa and Berryman 1979). When emergence from brood trees is synchronous, populations are more successful in overcoming the defenses of new host trees. 'Mass attacks', which increase population success, are driven by emergence synchrony which results from temperature control of life-cycle timing.

In low elevation lodgepole pine forests, a temperature regime that results in univoltinism (one generation per year) and synchronous summer emergence is predicted to be the most

successful for sustaining MPB outbreaks (Logan and Bentz 1999). With no known diapause to synchronize lifestages, MPB seasonality appears to be a direct consequence of nonlinear, stage-specific rate curves (relating temperature and rate of development) and thermal periodicity (Jenkins et al. 2001). Using development rate data collected at a range of constant temperatures, a lifestage-specific model of mountain pine beetle phenology was developed (Bentz et al. 1991) and later refined to include individual variability (Gilbert et al. 2004).

Within the past 5-10 years, wide-scale MPB caused mortality has occurred in high elevation pine stands throughout western North America and ongoing climate shifts are blamed (Logan and Powell 2001). Herein we describe MPB phenology in high elevation, seral whitebark pine forests in the Greater Yellowstone Ecosystem. Using field observations and phenology model predictions we explore how temperature changes may be influencing the ecological relationship between MPB and high elevation pines.

Methods

Research Sites and Data Collection

Phenological data were collected at three high elevation whitebark pine sites with MPB population levels ranging from endemic to outbreak (Table 1).

Table 1. Research sites located within the Greater Yellowstone Ecosystem predominated by whitebark pine.

Site Name	District, Forest	Elevation (m)	Coordinates
Black Butte	Madison Ranger District, Beaverhead-Deer Lodge, MT	2743	N 44.92036° W 111.82649°
Sawtell Peak	Island Park Ranger District, Targhee National Forest, ID	2652	N 44.55579° W 111.44157°
Togwotee Pass	Windriver Ranger District, Shoshone National Forest, WY	2926	N 43.74401° W 110.05324°

In June 2004, emergence cages were placed on ten whitebark pine at each site that had been attacked and infested by MPB in 2003. Emergence cages consisted of a flexible screen stapled over a 0.60 x 0.30 m section of the tree bole, centered at approximately 1.37 m height from the ground, one each on the north and south aspect of the bole. A tube attached to the bottom of the screen enclosure collected all adults that emerged from the tree bole within the sample space. In early June 2005, emergence cages were placed on ten trees at each site that had been infested during the summer and fall of 2004. All cages were checked weekly during the summers of 2004, 2005 and 2006. Due to the remoteness and difficult access of all sites, initial collections often did not occur until after emergence had commenced. Air temperature was recorded hourly at each site throughout each year beginning June 2004 and ending 30 September 2006 (Onset Computer, Bourne, MA, U.S.). Following emergence, bark

underneath each cage was removed and a variety of measurements taken, including the number of pupal chambers and parent adult mortality (Schen-Lagenheim unpublished data). The number of pupal chambers (e.g. new brood adults) was compared to number of adults collected from each cage providing a measure of parent adult re-emergence.

Mountain Pine Beetle Phenology Model
The MPB phenology model (MPBphen) describes development rate (the inverse of time required to complete a stadium) of eight MPB lifestages (ovipositional adult, egg, larval instars 1 – 4, pupae and teneral adult) as a function of temperature. The model was developed based on algorithms in Logan (1988) and parameterized using development rate data collected at six constant temperatures in the laboratory (Logan and Amman 1986, Bentz et al. 1991). Ovipositional adult development is based on equations and data described in Logan and Bentz (1999). Variability in individual development was included in the model based on the age-structured McKendrick-von Forester partial differential model (Gilbert et al. 2004). MPBphen is driven by hourly temperature and predicts the proportion of individuals in each lifestage throughout the lifecycle. The model used here is coded in the MATLAB (Math Works 2006) mathematical language. Field validation in low elevation lodgepole pines indicates the model does a very good job of predicting emergence timing (Bentz et al. unpublished data).

Model Evaluation and Simulations
MPBphen requires an input distribution of ovipositional adults and hourly temperature for the duration of the lifecycle (e.g. up to 3 years). To evaluate model predictions of MPB phenology in high elevation whitebark pine, we initiated the model with an input distribution of ovipositional adults based on observed timing of emergence in 2004 from trees infested in 2002 and 2003. Hourly air temperature data collected at each site were used to drive the model. Based on analyses in Bolstad et al. (1997), 1.8°C was added to each hour temperature to accommodate differences between air and phloem temperatures.

We were interested in using MPBphen to predict adult emergence timing at high elevation pine sites for years without observed temperature measurements. Herein, we present methods and results for only one site, Togwotee. Daily maximum and minimum temperatures were acquired for 10 NRCS SNOTEL stations (http://www.wcc.nrcs.usda.gov/snow) that were in close proximity and elevation to the Togwotee site. Using mixed model analyses (SAS Institute Inc.), parameters were estimated to predict daily maximum and minimum temperatures any given year using temperature data collected at the Togwotee site in 2004, 2005 and 2006, and data from the 10 SNOTEL sites. Daily maximum and minimum temperatures at the Togwotee site were then predicted for several years in the range of available data at the SNOTEL sites. A sine wave function was used to predict hourly temperatures from daily maximum and minimum temperatures. Field observations suggest that peak flight at the Togwotee site was centered around the middle of July. Therefore, an input distribution of ovipositional adults based on a normal distribution with a mean date = July 13 and standard deviation = 10 d was used for all simulation runs. Additional temperatures were predicted in a similar fashion for a whitebark pine site near Crater Lake in Oregon using SNOTEL stations at ~1820m.

Results and Discussion

Mountain Pine Beetle Emergence Timing

Patterns of adult emergence from trees attacked in 2004 was similar among the three sites. At all sites, adults emerged from individual trees both 1 and 2 years following attack. There was no consistent trend among the trees in proportion adults emerging each year. Some trees had a majority of 1 year beetles (e.g. univoltine) and other trees at the same site produced a majority 2 year beetles (semivoltine). Early peaks in emergence the first year following attack contained a least some proportion of parent adults that re-emerged. We assume these parents will attack new hosts and produce a second brood cohort, although the fate of re-emerged parents has not been studied in the field.

Using emergence cages similar to those used in the current study, Bentz (2006) observed adult emergence from low elevation lodgepole pine sites to be highly synchronized, with >90% of emergence occurring in a 14 d period. In the current study, at high elevation whitebark pine sites, emergence occurred over a period >60 d, particularly 1 year following 2004 attacks. We hypothesize that long emergence periods at high elevation sites is a function of the influence of temperature on lifestage timing, which in turn influences the overwintering lifestage(s). Similar patterns of dispersed summer MPB emergence were observed in western white pine (DeLeon et al. 1934).

Our results suggest that in high elevation whitebark pine a variety of cohorts may be emerging to attack trees at any given time. Cohorts comprising parent beetles, brood adults developing on a 1 year lifecycle and brood adults developing on a 2 year lifecycle could be emerging to attack new host trees at any given time. Given the large amount of whitebark pine mortality observed at our sites (Schen-Langenheim unpublished data), these results suggest that strict univoltinism, as is often observed in low elevation lodgepole pine sites, is not necessarily a requirement for mountain pine beetle population outbreaks at high elevation sites.

MPBphen Simulations

Using observed timing of beetle attacks in 2004 and observed hourly temperatures in 2004, 2005 and 2006, MPBphen did a good job of describing the proportion of beetles emerging 1 and 2 years following attack (Fig. 1).
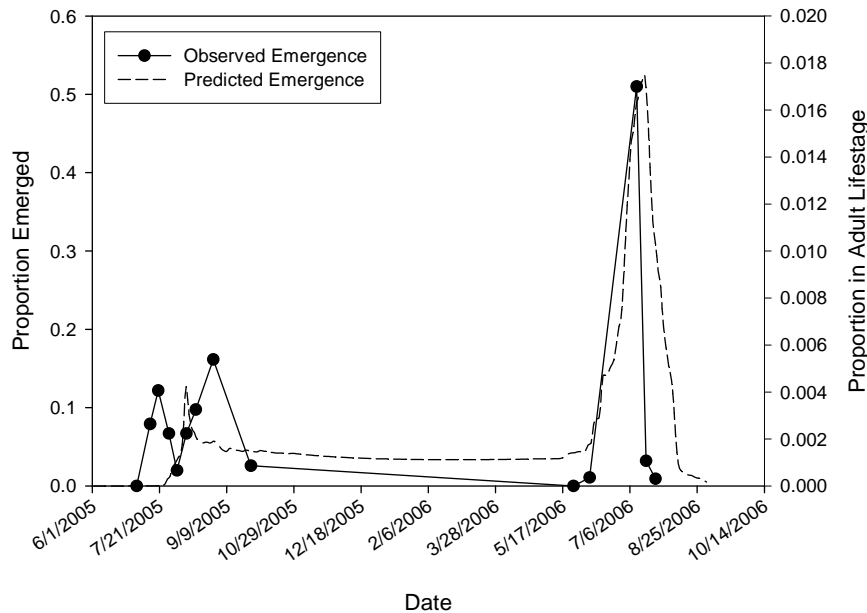

Figure 1. Observed and predicted MPB emergence from whitebark pine attacked in 2004. Proportion MPB emerged predicted using MPBphen and observed hourly temperatures recorded at the Togwotee field site. Observed emergence data collected using emergence cages on infested trees at the Togwotee site.

We then used MPBphen and predicted temperatures to estimate emergence timing at one site, Togwotte, for additional years. Using predicted temperatures to drive MPBphen, results suggest that trees attacked in 2003 would produce 100% 2 year beetles. Field observations indicated that trees attacked in 2004 produced a small proportion of 1 year beetles, with the majority developing in 2 years. However, trees attacked in 2005 were predicted to have a majority of 1 year beetles, with the remainder developing in 2 years. Therefore, MPBphen predictions and observed data suggest that warming temperatures from 2003 through 2006 resulted in a voltinism shift from a majority of MPB developing in 2 years to a majority of the population developing in 1 year. Additional simulations using temperatures predicted for the middle 1970s, when MPB outbreaks in whitebark pine were observed to be at low levels, estimated a large proportion of MPB developing on a 3 year lifecycle (Fig. 2).
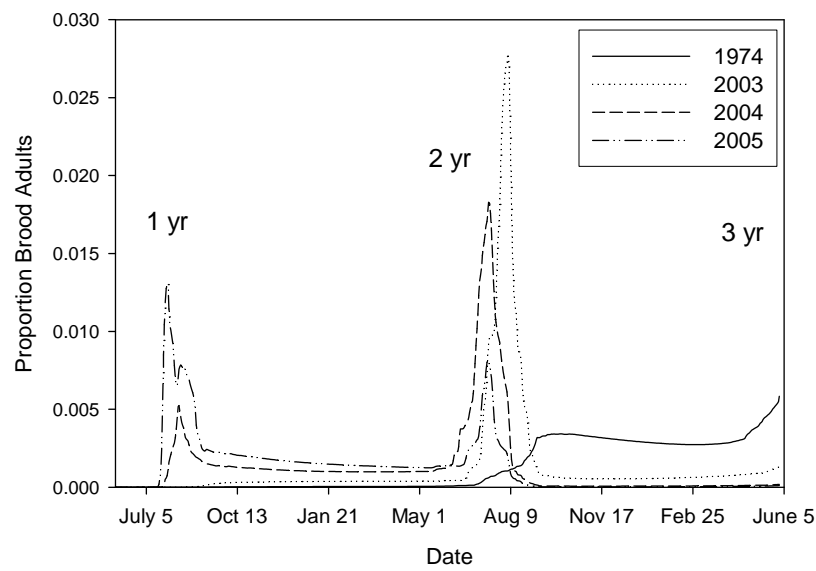
Figure 2. MPBphen predictions of MPB emergence timing at the Togwotee whitebark pine site. Shown are the proportion brood adults emerging in 1 and 2 years by year of tree attack. Brood not emerging in 1 and 2 years are assumed to emerge in 3 years.

Using predicted temperatures for a whitebark pine site at ~1820m near Crater Lake, Oregon, MPBphen predicted trees attacked in 2004 would produce 100% 1 year beetles. Similar results were obtained when MPBphen was run using predicted temperatures for trees attacked in 1989 at the same site. However, USDA Forest Service, Forest Health Protection, Aerial Detection Surveys indicate there has been a significant increase in whitebark pine mortality in Oregon between 1989 and 2004. This suggests that factors in addition to MPB voltinism, such as temperature effects on host trees, are undoubtedly influencing outbreak dynamics in high elevation whitebark pine forests across western North America.

Field observations and model predictions suggest that MPB development at high elevation sites is flexible and highly responsive to changes in temperature. A variety of voltinism pathways allow for population success and subsequent host tree mortality. Additional research is needed to better understand differences in temperature-driven phenology and subsequent attack strategies of MPB at low and high elevation pine sites. Predictions of continued climate change dictate a need for long term research investigating the differential role of temperature and host effects on MPB population success in high elevation whitebark pine ecosystems.

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